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Interannual variations of aboveground biomass and nutritional quality of Mediterranean grasslands in Western Spain over a 20-year period

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Running head: interannual variations of nutritional quality in pastures

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Abstract

The 'dehesas' are savannah-like semiarid grasslands typical of western Spain that are subject to strong inter-annual variations in biomass production. Over a 20-year period, from 1986 to 2005, aboveground biomass and the nutritional quality of these grasslands in the province of Salamanca (western Spain) were evaluated to determine the relationships between interannual variations in grassland parameters and climate variables (precipitation and temperature). Herbage samples were collected from several sites, along a topographic gradient that differentiated two types of herbaceous communities on the upper and lower part of the slope. Nutritional quality was assessed by determining on the basis of protein, acid detergent fibre, neutral detergent fibre, lignin and digestibility.

On both the upper and lower zones total biomass and biomass of grasses were correlated with annual precipitation calculated from the previous October to the current June. Biomass of legumes and forbs, on the upper zones, was correlated with spring precipitation. Stepwise multiple regression analysis provided different models for grasses, legumes, forbs and total biomass for the upper and lower zones. Protein concentration was negatively correlated with annual precipitation in both zones of slope. The number of days in spring with precipitation (≥ 1 mm or ≥ 10 mm) was a good predictor of the lignin content and digestibility in both zones of the slope, and of the acid detergent fibre content on the upper zones and the neutral detergent fibre content on the lower zones.

Additional keywords: 'dehesa'; pastures; protein; digestibility; temporal models; climate

Introduction

The grasslands of the western Iberian Peninsula form part of the 'dehesas', a semiarid ecosystem (savannah-like grasslands) that occupies more than $6 \cdot 10^6$ hectares. The term 'dehesa' has many meanings, although currently the most widely accepted definition is that of an agro-silvo-pastoral system developed on poor or non-agricultural land, that is used for open-range livestock raising. The pastures and vegetation of these Mediterranean systems are determined by two main characteristics: the Mediterranean nature of the climate (dry summers and cold winters) and the low fertility of the soil. With these and other difficulties, the 'dehesas' are an efficient example of how the management of large systems can be compatible with conservation and sustainable rural development (Olea and San Miguel 2006). These ecosystems must be managed with multiple objectives corresponding to the different functions assigned to grassland: environment, biodiversity, landscape ecology, and agricultural production with socio-economics outputs (Lemaire *et al.* 2005). 'Dehesas' are ecosystems that are maintained for open range exploitation and are of great value since they feature natural grasslands with high floristic diversity, an arbustive stratum, crops and sown pastures, livestock and hunted species.

Mediterranean ecosystems are characterized by strong seasonal and inter-annual variations in biomass production. Pasture production is a crucial aspect that sets the stage for other trophic levels (McNaughton *et al*. 1989) and is also useful for the appropriate management of such systems. Variations in aboveground biomass production of temperate grasslands have been positively correlated with abiotic factors; generally precipitation (Lauenroth and Sala 1992; Briggs and Knapp 1995; Xiangming *et al*. 1996; O´Connor *et al*. 2001; Nippert *et al*. 2006). Grassland quality in terms of nutritional value is a major determinant of animal production efficiency (van Soest 1982). However, little is known about interannual variations of nutritional quality, or relationships between quality and climate. Herbage quality is mainly determined by plant maturity, but plant environment modify the impact of herbage maturity on forage quality and cause year-to-year, seasonal and geographical location effects on forage quality even when harvested at the same stage of development (Buxton 1996). Plant environment often exerts its greatest influence on forage quality by altering leaf/stem ratios, but it also influences senescence rates or causes modifications in plant development and changes in chemical composition of plants. The most important environmental factors are temperature, water deficit, solar radiation and soil nutrient availability (Buxton and Fales 1994). High growth temperatures consistently reduce the digestibility of forages whether it be tropical or temperate, grass or legume, or leaf or stem (Ford *et al*. 1979; Wilson 1982; Wilson *et al*. 1991; Buxton and Fales 1994). There seems to be general agreement that plants growing in dry habitats have large amounts of structural tissue associated with low digestibility. However, most of the effects of water stress on forage quality are positive, although reports regarding the effect of drought on protein concentration have been contradictory (Wilson and Ng 1975; Buxton and Fales 1994).

The main objective of the present study was to analyse the interannual variations in biomass and nutritional quality, as indicated by protein, acid detergent fibre (ADF), neutral detergent fibre (NDF), lignin and digestibility (DMD), of semiarid grasslands in western Spain. We used data from a 20-year period (from 1986-2005) taken at several locations in the province of Salamanca. At each location a topographic gradient that differentiated herbaceous communities on the upper and lower zones of the slope was sampled. Previous reports have shown that upper and lower zones are different in biomass, mineral nutrient content and nutritional quality (Pérez Corona *et al*. 1995; Vázquez de Aldana *et al*. 1996; Pérez Corona *et al*. 1998). In this paper, specific hypothesis are that: 1) interannual variations in biomass and nutritional quality are related to variations in weather and 2) there is an interaction between slope position and weather as indicated by interannual variations in biomass and nutritional quality.

Materials and Methods

Study area

Research was conducted in the ‘dehesa’ area of the province of Salamanca (western Spain). This ecosystem occurs on gently undulating hills and features low-density *Quercus ilex* subsp. *rotundifolia* with seminatural grassland characterized by a complex floristic composition. The land is mainly used for the free range grazing of beef cattle and fighting bulls, although Iberian-bred pigs and game animals (deer, rabbits and hares) are also consumers of ‘dehesa*’* resources. The substrate is mainly siliceous, with many zones of slate or granite. Overall, the soils are distric Cambisols (García 1987). The climate is supra-Mediterranean, with cold winters and dry, warm summers.

These grasslands belong to geomorphologic units corresponding to slope-bed systems. A topographic gradient determines two extreme zones, the upper and the lower, which are connected by the vectorial transport of water and nutrients from the upper to the lower parts and may lead to the development of vegetation gradients (Puerto and Rico 1997).

Herbage sampling

Thirty gentle slopes were selected within the ‘dehesa*’* grasslands of the province of Salamanca (western Spain). These slopes are spread through the province within coordinates 40º 31’ – 41º 15’ N and 5º 20’ – 6º 29’ W. Slope lengths were about 100 m and the altitude differences ranged between from 15 to 25 m. On each slope, two topographically differentiated zones were determined: the uppermost and lowermost zones. Herbage samples were collected from those 30 locations from 1986 to 1993. From 1994 to 2005, five of the 30 previously selected slopes were selected and herbage samples were collected. In 1992, no sampling was carried out, and in 1986 and 1990 it was only possible to sample from the lower zone because most of the vegetation in the upper zone was dry.

Plant samples were collected at the end of the growing season (late May or early June) -the time of peak biomass (Pérez Corona 1992). Plants in the upper zone were at a slightly later stage of ripening than those from the lower zone. Sampling was accomplished by cutting the aboveground herbaceous vegetation in four randomly selected quadrats (0.25 m²) at 2 cm above ground level. Each sample was manually sorted into its main botanical components: grasses, legumes and forbs, and death tissue was removed. The most frequent plant species present in each group are listed in Table 1. Vegetation in the lower zones was characterized by a greater proportion of grass species and in the upper zones by a greater proportion of forbs. After sorting, samples were dried in a forced-air oven at 60 ºC for 48 h and weighed to determine biomass. Samples were ground in a Retsch mill with a 0.5 mm mesh sieve.

Table 1

Chemical analyses

Chemical analyses were performed on the community samples. Total biomass samples were analysed for crude protein using the Kjeldahl distillation method. Neutral detergent fibre (NDF), acid detergent fibre (ADF), lignin and dry matter digestibility (DMD) were analysed using the methods described by Goering and Van Soest (1970). All units are expressed on a dry matter basis.

Soil samples and analysis

Soil samples were collected with steel cylinders measuring 8 x 20 cm at each of the 30 locations and on the two slope positions in 1988. Samples were analysed for pH, organic matter, total N, total C, coarse and fine sand fractions, silt and clay as described previously (Vázquez de Aldana *et al.* 1996). Soil moisture was measured in five slopes.

Meteorological data

Meteorological data were obtained from several weather stations located close to the sampling locations (distance less than 10 km). From 1985 to 1993, data were obtained from eleven weather stations located close to the sampling locations (30 sites). From 1994 to 2005, data were obtained from three weather stations located close to the five sampling locations. The variables measured included daily temperature, daily minimum and maximum temperature, and daily precipitation.

The average annual rainfall from 1986-2005 was 580 mm, with considerable monthly variation (Fig. 1). Highest precipitation was recorded in October with a mean of 91 mm over the 20-year period. Summer precipitation mainly occurred in September. Mean monthly temperatures ranged from 4.2 ºC in January to 21.4 ºC in July.

The data were used to develop climate variables for each year from 1986-2005. Annual precipitation was calculated from 1 October of the year prior to sampling to 30 June of the sampling year (current year), which was the month when plant samples were collected (P_{oct_jun}); seasonal precipitation (P_{aut}, P_{win}, P_{spr}, P_{sum}); monthly precipitation (P_{mon}); number of days with precipitation ≥ 1 mm (annual and seasonal,, DP); number of days with precipitation ≥ 10 mm (annual and seasonal, DP10); number of days with precipitation ≥ 100 mm (annual and seasonal, DP100); mean monthly daily temperature (TM); mean monthly maximum daily temperature (TMMAX); mean monthly minimum daily temperature (TMMIN); number of days with minimum temperature ≤ 0 ºC (DT0). The variables corresponding to the autumn months refer to those of the year prior to the sampling year.

During the period of highest plant growth, solar radiation varied between 459.5 Mj/m^2 in March (7.8% on annual basis) and 755.9 Mj/m^2 in June (12.8% on annual basis). These data were available from one weather station for a three-year period (2003-2005).

Fig.1

Statistical analyses

The data were analysed statistically by two-way analysis of variance for the effects of slope zone, sampling year and their interaction on biomass production and nutritional quality parameters.

The association between individual climate variables and biomass production and herbage quality parameters was estimated for each slope zone using correlation analysis. Analysis of the interrelationships among multiple variables was performed by step-wise multiple regression analysis. In the case of quality parameters, we also included as independent variables (predictors) the percentage (dry weight) of grasses, legumes and forbs in the total biomass. These correlations and multiple regression analyses were performed on the data matrix of the means of the sampling sites and the means from the weather stations considered for each of the years. The models with multiple predictors were tested for co-linearity by means of Durbin-Watson test, for autocorrelation among residuals, and FIV and tolerance statistics for co-linearity. All statistical analysis were performed using the analytical software SPSS (version 13.0.1, Chicago, Illinois)

Results

Biomass

On the upper zones mean biomass ranged between 50.4 g/m^2 (in 1997) to 214 g/m^2 (in 1998) (Fig. 2). Total mean biomass (125 g/m^2) was mainly composed of forbs (62.8 g/m^2) and grasses (47.9 g/m^2), being legumes the minority group (18.9 g/m^2). On the lower zones, mean biomass ranged between 148 g/m^2 (in 2002) to 419 g/m^2 (in 1996). Mean biomass (288 g/m^2) was mainly composed of grasses (183 g/m^2), followed by legumes (59.2 g/m^2) and forbs (47.4 g/m^2).

Upper zones had significantly ($P < 0.001$) greater biomass of forbs and lower biomass of legumes, grasses and total than the lower zones (Table 2). There were significant ($P < 0.001$) differences in biomass among sampling years (Fig. 2). Biomass on the upper zones was significantly correlated to that on the lower zones along sampling years for grasses ($r = 0.656$; $P = 0.008$; $n = 15$), legumes ($r = 0.549$; $P = 0.034$; $n = 15$) and total biomass ($r = 0.574$; $P = 0.020$; $n = 16$), but not in forbs ($r = 0.251$; $P = 0.366$; $n = 15$).

Figure 2

Table 2

Nutritional quality

There were significant differences ($P < 0.001$) in nutritional quality (protein, ADF, NDF, lignin and DMD concentrations) among sampling years. On the upper zone, the highest mean protein concentration was recorded in 1991 when the NDF, ADF and lignin contents were the lowest and digestibility was the highest (Fig. 3). The lowest mean protein content was recorded in 1996 when the NDF and ADF contents were the highest. On the lower zone, the highest mean protein concentration and digestibility were also recorded in 1991 when the NDF, ADF and lignin concentrations were the lowest. The lowest protein content was recorded in 1988, when the ADF and lignin were the highest (Fig. 3).

Protein and NDF concentrations and digestibility were statistically significantly ($P < 0.001$) greater on the lower than on the upper zones (Table 2). On the other hand, lignin and ADF contents were significantly ($P < 0.01$) greater on the upper than in the lower zones (Table 2). Among nutritional quality along sampling years there were significant correlations between upper and lower slope zones for: protein ($r = 0.794$; $P = 0.000$; $n = 17$), neutral detergent fibre ($r = 0.862$; $P = 0.000$; $n = 17$), acid detergent fibre ($r = 0.891$; $P = 0.000$; $n = 17$), lignin ($r = 0.537$; $P = 0.026$; $n = 17$), and dry matter digestibility ($r = 0.754$; $P = 0.000$; $n = 17$).

Figure 3

Relationships between biomass and climate variables

On both the upper and lower zones total biomass was positively and significantly ($P < 0.05$) correlated with the annual precipitation calculated from the previous October to the current June and with the previous autumn precipitation (Table 3; Fig. 4). There was a significant ($P < 0.05$) positive correlation between biomass on the upper zone and the number of days with appreciable precipitation in spring (DP_{spr}), but not between biomass and total spring precipitation. On both zones biomass was also significantly and positively correlated with DP_{oct_jun} and DP_{aut}. There were significant and positive correlations between biomass and several temperature variables corresponding to November and December (from the autumn prior to the sampling year): TM_{nov_pre}, TM_{dec_pre}, $TMMIN_{nov\_pre}$ and $TMMIN_{dec\_pre}$ (Table 3); and negative correlation with the number of days with frost in those months (Fig. 4).

Table 3

Fig. 4

Biomass of grasses was positively and significantly ($P < 0.05$) correlated with annual precipitation (P_{oct_jun}) in both slope zones and with autumn precipitation in the upper zones (Table 3). On the upper zones biomass of legumes and forbs was positively and significantly ($P < 0.05$) correlated with spring precipitation. On the lower zones, several variables related to the autumn temperature such as TM_{nov_pre}, TM_{dec_pre}, $TMMIN_{nov\_pre}$ and $TMMIN_{dec\_pre}$ were significantly ($P < 0.05$) correlated with grasses, legumes and forbs biomass (Table 3). However, in the upper zones there were only significant correlations ($P < 0.05$) between biomass of forbs and $TMMIN_{nov\_pre}$. The $DT0_{nov\_pre}$ variable was significantly ($P < 0.05$) and negatively correlated with biomass of grasses and legumes in the lower zones and with biomass of forbs in both zones.

Stepwise multiple regression analysis provided different models for year-to-year biomass variation depending on the slope zone (Table 4). On the lower zones, annual precipitation (Poct-jun) and TMMIN of previous December or November explained most of the interannual variations of biomass of grasses and total biomass. On the upper zones, total biomass was best explained in terms of the number of days with an annual precipitation of ≥ 1 mm (DP_{oct_jun}) and total precipitation in April, and biomass of grasses in terms of $DP_{oct-jun}$ (Table 4). The interannual variations of legumes and forbs were partly accounted for (38% and 57% of the variance, respectively) by the mean November temperature variable (TM_{nov_pre}) on the lower zones. On the upper zones biomass depended on precipitation variables, thus monthly precipitation in April accounted for 62% of the variations of legumes, and the number of days per year (DP_{oct_jun}) and in spring (DP_{spr}) with precipitation explained 70% of the variations in forbs biomass.

Table 4

Relationships between nutritional quality and climate variables

Protein concentration was significantly and negatively correlated with the annual precipitation (P_{oct_jun}) in both slope zones (Table 5). Furthermore, on the upper zones protein was significantly (P < 0.05) and negatively related to winter precipitation Table 5) and to other precipitation climate variables, such as the number of days per year with a precipitation above 1 mm (r = –0.508; P = 0.037), precipitation ≥ 10 mm (r = –0.492; P = 0.045), precipitation ≥ 100 mm (r = –0.753; P = 0.000), and with the number of days in winter with a precipitation above 1 mm (r = –0.570; P = 0.570), precipitation ≥ 10 mm (r = –0.584; P = 0.014) and precipitation ≥ 100 mm (r = –0.629; P = 0.007).

Table 5

Spring precipitation and other similar variables (monthly precipitation of May, number of days in spring with precipitation ≥ 10 mm and ≥ 100 mm) were significantly (P < 0.05) and positively correlated with the ADF and lignin concentrations, and negatively correlated with DMD in the upper zones (Table 5). For the lower zones, these correlation coefficients were not statistically significant (P > 0.05), except between DMD and $DP10_{spr}$. Concentration of NDF was not significantly correlated (P >

0.05) with any of the climate variables. No significant correlations (P > 0.05) were found between nutritional quality parameters and the temperature variables.

The results of the stepwise multiple regression analysis concerning the interannual variation in protein concentration provided models with the same predictive variable for both zones ($DP100_{oct\_jun}$), the R^2 regression coefficient being higher for the upper zones than for the lower ones (Table 6). Most of the interannual variations in the fibre and digestibility parameters can be explained in terms of the number of days in spring with precipitation (DP_{spr} and $DP10_{spr}$).. In the cases of lignin and DMD, the same variables appeared in the models of the upper and lower zones, and for both parameters higher R^2 coefficients were obtained for the upper zones. On the lower zones interannual variation in the concentration of ADF can be explained by the number of days from October to June with appreciable precipitation (DP_{oct_jun}), and in the upper zones by the number of days in spring with precipitation ≥ 10 mm ($DP10_{spr}$). Regarding NDF concentration, interannual variations in the lower zones were explained by the percentage of grasses (dry weight) in total biomass and the number of days in spring with precipitation ≥ 10 mm ($DP10_{spr}$) (Table 6). For the upper zones, no significant model (P > 0.05) able to explain the interannual variations in the chemical composition was obtained.

Table 6

Discussion

Here we report that interannual variations in biomass and nutritional quality of semiarid pastures of the ‘dehesa’ ecosystem are related to climate, as hypothesized. For each of the parameters analysed, significant correlations were observed along the sampling years between upper and lower zones. In principle, this suggests similar models of interannual variation for both zones of the slope. However, on considering the different climate variables to explain such interannual variations, we observed that models of variation of biomass and several nutritional quality parameters were dependent on the topographic gradient.

On both the upper and lower zones of slope interannual variations in biomass were found to be significantly correlated with annual precipitation (P_{oct_jun}) and with seasonal precipitation of the autumn prior to the sampling year (P_{aut}). The relationship between biomass production in grasslands and precipitation has been reported by several authors, referred to different periods of the year: annual precipitation from January to December (Lauenroth and Sala 1992; Briggs and Knapp 1995), precipitation of the previous year (Oesterheld *et al.* 2001) current-year spring precipitation and previous-year spring precipitation (Smart *et al.* 2007). Wiegand *et al.* (2004) found that interannual variation in the phytomass production of semiarid grasslands in South Africa is explained by current-year precipitation and a memory index that combines mean monthly temperature and precipitation of the previous four years.

In the present work we failed to find any significant correlation between biomass production and total annual precipitation considered from January to December of the sampling year nor when considered from January to June. However, on considering annual precipitation from October of the year prior to sampling to June a linear relationship was found with the biomass of the lower and upper zones, which indicates the importance of autumn precipitation for biomass in these grasslands. The autumn precipitation is of crucial importance in the germination of the species of the seed bank in Mediterranean pastures of semiarid zones (Espigares and Peco 1993; Peco *et al.* 1998). In autumn, the first rains initiate germination and grassland regrowth; a drought after the first autumn rains exerts a significant effect on the floristic composition of the annual pasture, mainly due to the differential effect on seedling mortality and hence, in the long run, on production.

We found different relationships between biomass and climate variables for the upper and lower zones. Herbage production from different plant communities undergoing the same climate inputs may not necessarily respond in the same way (Smart *et al.* 2007). Significant correlations were found with precipitation in April (for legumes and forbs) and with the number of days in spring with appreciable precipitation (for total biomass) in the communities of the upper zone but not in those of the lower zone (Table 3). The slopes on which the sampling was carried out are characterised by a variation in water and nutrient availability, which define a gradient from the upper to the lower zones. Soils on upper zones had lower soil moisture (12.3%) organic matter (3.67%), total nitrogen (0.18%), silt (23.2%), clay (16.2%) and higher coarse sand (36.9%) and fine sand (23.4%) as compared to lower zones: water 19.1%, organic matter 5.7%, total nitrogen 0.27%, silt 36.3%, clay 23.1%, coarse sand 17.4% and fine sand 23.4% (Non published data). Thus, communities on the upper zone of slope, with a lower soil moisture and organic matter contents seem to be more susceptible to variations in precipitation at certain critical times, such as in April, when biomass production begins to increase after the winter halt, while on the lower zones of the slope, where moisture remains longer, biomass is not affected by that variation. Similarly, these differences in soil characteristics between slope zones would explain why variables such as the number of days of precipitation (DP_{oct_jun}; DP_{apr}) are more important than total precipitation in explaining interannual variation of biomass on the upper zones (from stepwise multiple regression analysis). In these semiarid ecosystems, it seems that biomass on the upper zones, with lower soil moisture content, would be favoured by the persistence of the soil moisture produced due to the precipitation of several days rather than by the total amount fallen during those days. Similar results have recently been published by Swemmer *et al*. (2007), who also highlight the importance of the distribution of precipitation as compared with the total amount fallen in production models of South African temperate grasslands.

When botanical components were considered separately, biomass of grasses, legumes and forbs responded differently to the climate variables. The interannual variability in biomass of grasses was correlated with P_{oct_jun} on both slope zones, and biomass of legumes and forbs with spring precipitation on the upper zones. Grasses, the dominant group in the lower zones, displayed a model of variation similar to that of total biomass; and the model of forb biomass, the dominant group on the upper zones, was similar to that of total biomass. Proportion of grasses (dry weight) in total biomass was negatively correlated with proportion of forbs (r = −0.602; P = 0.018), suggesting a competition factor between the species of both groups. Forb growth is favoured when soil moisture conditions are poor, suggesting that forbs are more limited by biotic interactions (competition) than by abiotic factors, that is, when water stress reduces grass production, forb production may respond positively to the reduction in competition (Briggs and Knapp 1995). The prediction model for grasses, legumes and forbs resulting from stepwise regression analysis included variables of temperature in the lower zones (Table 5). In a study carried out to examine the variations in production at species level and at regional scale, Epstein *et al*. (1998) found that mean annual temperature was the most important variable in species prediction models. Similarly, in other works no significant relationships were found between forb production and precipitation variables (Briggs and Knapp 1995; Nippert *et al*. 2006).

Regarding nutritional quality, we found a negative relationship between protein concentration in herbage and annual precipitation (P_{oct_jun}), furthermore all relationships between protein and precipitation variables were negative although not significant. These results agree with those of Griffin and Watson (1982) in bermudagrasses but not with Kuusela (2004) in clover-grass mixtures; results of Perterson *et al.* (1992) about the effects of drought on protein contents of legumes were not consistent.

Protein content of plants may vary: (I) with plant growth, as a dilution effect; and (II) with soil mineralization. These two factors are subjected to variation with climate (precipitation and temperature). On the other hand, NDF, ADF and lignin concentrations are also affected by plant growth and they increase with plant biomass that is the inverse of dilution effect for protein content. (I) Plant environment exerts its greater influence over herbage quality by altering rate of plant development and leaf/stem ratios (Buxton and Fales 1994). A rise in temperature normally increases rate of plant development and in so doing increase lignification and decrease nitrogen concentration and digestibility. Water stress with minimal associated heat stress often improves forage nutritive quality because moisture stress slows maturation of forages and delays stem development, resulting in increases in the concentration of nitrogen and leafier swards with lower lignification and higher digestibility (Wilson 1982; Nelson and Moser 1994). (II) Low soil moisture limits metabolic activity of the microorganisms´ enzyme systems, and as soil moisture levels rise, metabolic activity increases until an optimum plateau is reached (Couteaux *et al*. 1995). Additional water does not affect metabolism until anaerobic conditions arise. At this point the decomposition rates of some biochemical compounds are reduced. In these Mediterranean grassland ecosystems where litter decomposition is mainly moisture limited, an increase of rainfall that increases soil moisture levels, would increase metabolic activity of microorganims (Couteaux *et al.* 1995).

Therefore, low herbage biomass due to low temperature or rainfall should lead to plants having higher protein concentration and digestibility, and lower NDF, ADF and lignin concentration, while favourable plant growth conditions should lead to the inverse. But at the same time, high soil moisture levels and high temperature can increase the N nutrition level of plant and then lead to an increase to protein content. Our results showed a negative correlation between annual precipitation and protein content in herbage, which suggests that the dilution effect is more important than the effect on plant N nutrition (by soil mineralization). This is also supported by the significant negative correlation between total biomass and protein content for the lower zone ($r = –0.301$, $P = 0.000$, $n = 334$). Such a correlation was not significant in the upper zone, suggesting that the effect of dilution is more important in the lower zone with higher biomass and greater proportion of grasses than in the uppers. In the lower zones pasture is mainly made up of grasses (Table 2), thus protein concentration of herbage was negatively correlated not only with total biomass, as previously indicated, but also with biomass of grasses (r = –0.490, P = 0.000, n = 319); and on the other hand, it was positively correlated with biomass of legumes (r = 0.229, P = 0.000, n = 319). On the upper zone grasses comprised a 38% of total biomass and there was not significant correlation between protein content of herbage and biomass of grasses.

Legumes component in pasture is an important factor in the protein concentration of herbage, since this botanical component have much greater protein concentration than grasses or forbs (Vázquez de Aldana *et al.* 2000). Several studies have shown that protein concentration in a grass-legume mixture is positively and linearly related to the legumes proportion (Mallarino and Wedin 1990; Kuusela 2004). We found an inverse relationship between proportion of legumes and proportion of grasses in the pasture ($r = -0.764$; $P = 0.001$; in the upper zones; $r = -0.945$; $P = 0.000$; in the lower zones); therefore, the increase in precipitation that leads to an increase in biomass production also means a decrease in the proportion of legumes, and hence a lower protein content in the herbage.

Regarding fibre contents our results showed really the inverse of the effect for protein. We found that several variables related to the spring precipitation (P_{spr}, P_{apr}, P_{may}, $DP10_{spr}$, $DP100_{spr}$) were positively and significantly correlated with ADF and lignin contents, and negatively with DMD. Previous reports also found that drought reduced ADF and NDF, and high quality of droughted forage was associated with delayed maturity (Wilson 1983; Peterson *et al*. 1992). The increase in biomass due to spring rainfall leads to herbage with higher fibre contents and consequently lower digestibility. Thus, there were significant correlations between total biomass and ADF (r = 0.428, P = 0.000, n = 334), NDF (r = 0.195, P = 0.000, n = 319) and lignin contents (r = 0.399, P = 0.000, n = 334) on the lower zone. In the upper zones these correlations were not statistically significant for total biomass ($P > 0.05$), but they were significant for biomass of grasses and that of forbs. Similar to the effect for protein content, lower zones with greater biomass are more sensitive to these variations in fibre contents; on the other hand, there is an inverse relationship between proportion of grasses and forbs in herbage (r = –0.602, *P* = 0.018, n = 15 on the upper zone; r = –0.491, *P* = 0.045, n = 15 on the lower zone), and grasses have greater NDF and lower lignin than forbs (Vázquez de Aldana *et al*. 2000). Therefore, an increase in spring precipitation that leads to an increase in biomass of forbs in the upper zones (Table 3), entails a decrease in the proportion of grasses which means a decrease in the botanical component with lower lignin concentration, and as a result lignin content in herbage increase.

No significant correlations were found between nutritional quality parameters and temperature variables. According to Wilson (1982) temperature is the most important environmental influence on herbage quality, because high temperatures accelerate growth. It has been reported that digestibility of grass tops decreases about 0.5% units per ºC increase in temperature, legumes may be a little less sensitive (Wilson 1982). Mean monthly temperature in May was 13.5 ºC (standard deviation = 0.93) and in April was 9.4 ºC (standard deviation = 1.3) during the 20-years period. This suggests that interannual variations in temperature are not strong enough to provoke changes in concentration of nutritional quality parameters in our pastures.

Although several correlation coefficients with climate variables were significant in the upper, but not the lower zones, the models of interannual variations of protein, lignin, and DMD, obtained by step-wise multiple regression analysis revealed the same variables in both zones of the slope. In the case of variations in ADF, similar variables were found for both zones, related to the number of days of precipitation. This suggests that the factors eliciting the differences between both zones as regards the concentration of quality are affected in the same way by the climate factors that cause the interannual variations.

Conclusion

The annual precipitation calculated from October of the year prior to sampling to June of the current year is a variable that determines part of the interannual variations in total and grasess biomass of the semi-arid pastures of the ‘dehesa’ ecosystem. This indicates the importance of the autumn rains in the interannual variations of the biomass of these grasslands. Several variables related to the spring precipitation accounted for some of the interannual variations of the NDF, ADF, lignin and digestibility parameters.

The communities of the upper and lower zones followed different models of variation, both as regards total biomass and botanical groups of grasses, legumes and forbs. The interannual variations in the nutritional quality explained by climate variables affect the communities of both zones of the slope in a similar way, however several correlation coefficients between weather and nutritional quality were significant in the upper but not in the lower zones.

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Table 1. Frequent plant species of the ‘dehesa’ grasslands

Botanical group	Species
Grasses	*Agrostis castellana* Boiss. & Reut.
	Anthoxanthum aristatum Boiss
	Bromus hordaceus L.
	Cynosurus cristatus L.
	Dactylis glomerata L.
	Festuca rubra L.
	Holcus lanatus L.
	Poa bulbosa L.
	Poa pratensis L.
	Vulpia bromoides (L.) Gray
Legumes	*Anthyllis lotoides* L.
	Lotus corniculatus L.
	Ornithopus compressus L.
	Trifolium arvense L.
	Trifolium dubium Sibth.
	Trifolium hybridum L.
	Trifolium pratense L.
	Trifolium striatum L.
	Trifolium subterraneum L.
Forbs	*Anthemis* spp.
	Cerastium glomeratum Thuill.
	Hypochoeris radicata L.
	Plantago lanceolata L.
	Ranunculus bulbosus L.
	Thapsia villosa L.
	Tolpis barbata (L.) Gaertn.
	Tuberaria guttata (L.) Fourr.

Table 2. Summary statistics for biomass and chemical composition of semiarid grasslands on the upper and lower slope zones for the period 1986-2005.

P-value indicates significant differences between zones

	Mean	Minimum value	Maximum value	Coefficient of variation (%)	P-value
Total biomass (g/m^2)					
Upper	125	20.5	514	58.7	0.000
Lower	288	50.9	894	43.9	
Grasses biomass (g/m^2)					
Upper	47.9	0	218	94.4	0.000
Lower	183	15.6	636	52.4	
Legumes biomass (g/m^2)					
Upper	18.9	0	128	135	0.000
Lower	59.2	0	274	92.4	
Forbs biomass (g/m^2)					
Upper	62.8	0.3	239	67.3	0.001
Lower	47.4	0	411	92.2	
Protein (g/kg)					
Upper	96.5	49.9	148	19.5	0.000
Lower	117	42.7	206	24.1	
NDF (g/kg)					
Upper	504	280	718	16.1	0.000
Lower	539	319	755	13.3	
ADF (g/kg)					
Upper	343	235	485	11.2	0.003
Lower	331	191	460	12.5	
Lignin (g/kg)					
Upper	54.5	23.7	122	30.8	0.000
Lower	39.2	18.3	86.5	28.6	
DMD (g/kg)					
Upper	631	477	736	7.69	0.000
Lower	667	555	796	6.90	

Table 3. Pearson's correlation coefficients between biomass and climate variables

Significant correlations (*P* < 0.05) are highlighted in bold. Significance level is shown in brackets.

	Total biomass		Grass biomass		Legume biomass		Forb biomass	
	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower
P_{oct_jun}	**0.541 (0.030)**	**0.672 (0.002)**	**0.518 (0.048)**	**0.667 (0.003)**	0.243 (0.382)	0.271 (0.294)	0.463 (0.082)	0.264 (0.306)
P_{aut_pre}	**0.532 (0.034)**	**0.551 (0.018)**	**0.642 (0.010)**	0.461 (0.062)	0.168 (0.550)	0.391 (0.121)	0.492 (0.063)	0.310 (0.226)
P_{spr}	0.102 (0.707)	0.228 (0.362)	−0.144 (0.609)	0.215 (0.407)	**0.630 (0.012)**	0.032 (0.903)	**0.522 (0.046)**	0.065 (0.803)
DP_{oct_jun}	**0.696 (0.003)**	**0.642 (0.004)**	**0.739 (0.002)**	**0.701 (0.002)**	0.248 (0.372)	0.168 (0.519)	**0.545 (0.036)**	0.205 (0.431)
DP_{spr}	**0.523 (0.038)**	0.121 0.633	0.065 0.817	0.078 0.765	**0.784 0.001**	0.226 0.382	**0.741 0.002**	0.059 0.822
TM_{nov_pre}	0.370 (0.158)	**0.722 (0.001)**	0.140 (0.619)	0.463 (0.071)	0.220 (0.431)	**0.616 (0.011)**	0.465 (0.080)	**0.756 (0.001)**
TM_{dec_pre}	0.419 (0.107)	**0.820 (0.000)**	0.475 (0.087)	**0.743 (0.001)**	0.086 (0.762)	**0.498 (0.050)**	0.399 (0.141)	**0.524 (0.037)**
$TMMIN_{nov\_pre}$	**0.579 (0.019)**	**0.823 (0.000)**	0.407 (0.132)	**0.623 (0.010)**	0.261 (0.347)	**0.604 (0.013)**	**0.561 (0.030)**	**0.665 (0.005)**
$TMMIN_{dec\_pre}$	0.425 (0.100)	**0.808 (0.000)**	0.478 (0.072)	**0.769 (0.000)**	0.098 (0.729)	0.479 (0.060)	0.438 (0.103)	**0.494 (0.050)**
$DT0_{nov\_pre}$	**−0.603 (0.013)**	**−0.783 (0.000)**	−0.309 (0.263)	**−0.554 (0.026)**	−0.404 (0.135)	**−0.661 (0.005)**	**−0.656 (0.008)**	**−0.651 (0.006)**

P_{oct_jun} = annual precipitation from October of the previous year to June.
P_{aut_pre} = precipitation of autumn of previous year.
P_{spr} = precipitation in spring.
DP_{oct_jun} = number of days from October of the previous year to June with precipitation ≥ 1 mm.
DP_{spr} = number of days in spring with precipitation ≥ 1 mm.
TM_{nov_pre} = mean monthly daily temperature of previous November.
TM_{dec_pre} = mean monthly daily temperature of previous December.
$TMMIN_{nov\_pre}$ = mean monthly minimum daily temperature of previous November.
$TMMIN_{dec\_pre}$ = mean monthly minimum daily temperature of previous December.
$DT0_{nov\_pre}$ = number of days with minimum temperature ≤ 0 ºC in November of previous year.

Table 4. Results of stepwise multiple regression analysis between grassland biomass and climate variables

Dependent variable	Model	R^2	*P*
Total DM lower	$125 + 0.161\ P_{oct\_jun} + 24.8\ TMMIN_{nov\_pre}$	0.734	0.000
Total DM upper	$-49.8 + 1.94\ DP_{oct\_jun} + 0.671\ P_{apr}$	0.642	0.001
Grasses DM lower	$115 + 0.123\ P_{oct\_jun} + 1.09\ TMMIN_{dec\_pre}$	0.634	0.001
Grasses DM upper	$-14.9 + 0.992\ DP_{oct\_jun}$	0.546	0.002
Legumes DM lower	$-41.2 + 1.15\ TM_{nov\_pre}$	0.380	0.011
Legumes DM upper	$-3.25 + 0.361\ P_{apr}$	0.623	0.000
Forbs DM lower	$-28.39 + 0.933\ TM_{nov\_pre}$	0.572	0.001
Forbs DM upper	$-20.6 + 1.71\ DP_{spr} + 0.566\ DP_{oct\_jun}$	0.708	0.001

DM = dry matter
P_{oct_jun} = annual precipitation from October of the previous year to June.
P_{apr} = precipitation in April.
DP_{oct_jun} = number of days from October of the previous year to June with precipitation ≥ 1 mm.
DP_{spr} = number of days in spring with precipitation ≥ 1 mm.
TM_{nov_pre} = mean monthly daily temperature of previous November.
$TMMIN_{nov\_pre}$ = mean monthly minimum daily temperature of previous November.
$TMMIN_{dec\_pre}$ = mean monthly minimum daily temperature of previous December.

Table 5. Pearson´s correlation coefficients between quality parameters and climate variables

Significant correlations (P < 0.05) are highlighted in bold. Significance level is in shown brackets.

	Protein		NDF		ADF		Lignin		DMD	
	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower
P_{oct_jun}	**−0.747**	**−0.497**	0.058	0.121	0.212	0.364	0.304	0.318	0.192	−0.327
	(0.001)	**(0.030)**	(0.826)	(0.621)	(0.413)	(0.126)	(0.235)	(0.184)	(0.460)	(0.172)
P_{win}	**−0.619**	−0.351	−0.290	−0.177	−0.255	−0.178	−0.289	−0.278	0.406	0.349
	(0.008)	(0.140)	(0.259)	(0.467)	(0.323)	(0.466)	(0.260)	(0.249)	(0.106)	(0.144)
P_{spr}	−0.229	−0.205	0.269	0.157	**0.478**	0.277	**0.753**	0.376	**−0.663**	−0.374
	(0.377)	(0.399)	(0.297)	(0.520)	**(0.050)**	(0.251)	**(0.000)**	(0.113)	**(0.004)**	(0.115)
P_{apr}	−0.019	−0.203	−0.036	−0.085	0.286	0.050	**0.554**	0.215	−0.440	−0.148
	0.(943)	(0.405)	(0.892)	(0.730)	(0.266)	(0.840)	**(0.021)**	(0.377)	(0.077)	(0.546)
P_{may}	−0.239	−0.011	0.434	0.320	**0.493**	0.309	**0.502**	0.211	**−0.477**	−0.316
	(0.355)	(0.963)	(0.081)	(0.182)	**(0.044)**	(0.198)	**(0.040)**	(0.385)	**(0.050)**	(0.187)
$DP10_{spr}$	0.060	−0.039	0.346	0.289	**0.573**	0.434	**0.734**	**0.485**	**−0.689**	**−0.466**
	(0.818)	(0.876)	(0.174)	(0.231)	**(0.016)**	(0.064)	**(0.001)**	**(0.035)**	**(0.002)**	**(0.044)**
$DP100_{spr}$	−0.227	−0.078	0.285	0.198	**0.486**	0.219	**0.717**	0.268	**−0.597**	−0.291
	(0.380)	(0.750)	(0.268)	(0.416)	**(0.048)**	(0.386)	**(0.001)**	(0.268)	**(0.011)**	(0.226)

P_{oct_jun} = annual precipitation from October of the previous year to June.
P_{spr} = precipitation in spring.
P_{win} = precipitation in winter.
P_{apr} = precipitation in April.
P_{may} = precipitation in May.
$DP10_{spr}$ = number of days in spring with precipitation ≥ 10 mm.
$DP100_{spr}$ = number of days in spring with precipitation ≥ 100 mm.

Table 6. **Results of stepwise multiple regression analysis between grassland quality parameters and climate variables**

Dependent variable	Model	R^2	*P*
Protein lower	$142 – 1.76\ DP100_{oct\_jun}$	0.249	0.041
Protein upper	$124 – 1.76\ DP100_{oct\_jun}$	0.636	0.000
NDF lower	$254 + 3.90\ Gra\% + 2.00\ DP10_{spr}$	0.644	0.001
NDF upper	No significant model		
ADF lower	$278 + 0.822\ DP_{oct\_jun}$	0.234	0.049
ADF upper	$316 + 1.56\ DP10_{spr}$	0.328	0.016
Lignin lower	$31.1 + 0.387\ DP_{spr}$	0.243	0.032
Lignin upper	$37.3 + 0.849\ DP_{spr}$	0.667	0.000
DMD lower	$695 – 1.74\ DP10_{spr}$	0.217	0.044
DMD upper	$687 – 3.02\ DP10_{spr}$	0.563	0.001

DP_{oct_jun} = number of days from October of the previous year to June with precipitation ≥ 1 mm.
$DP100_{oct\_jun}$ = number of days from October of the previous year to June with precipitation ≥ 100 mm.
DP_{spr} = number of days in spring with precipitation ≥ 1 mm.
$DP10_{spr}$ = number of days in spring with precipitation ≥ 10 mm.
$DP100_{spr}$ = number of days in spring with precipitation ≥ 100 mm.
Gra% = Proportion (in dry weight) of grasses in total biomass.

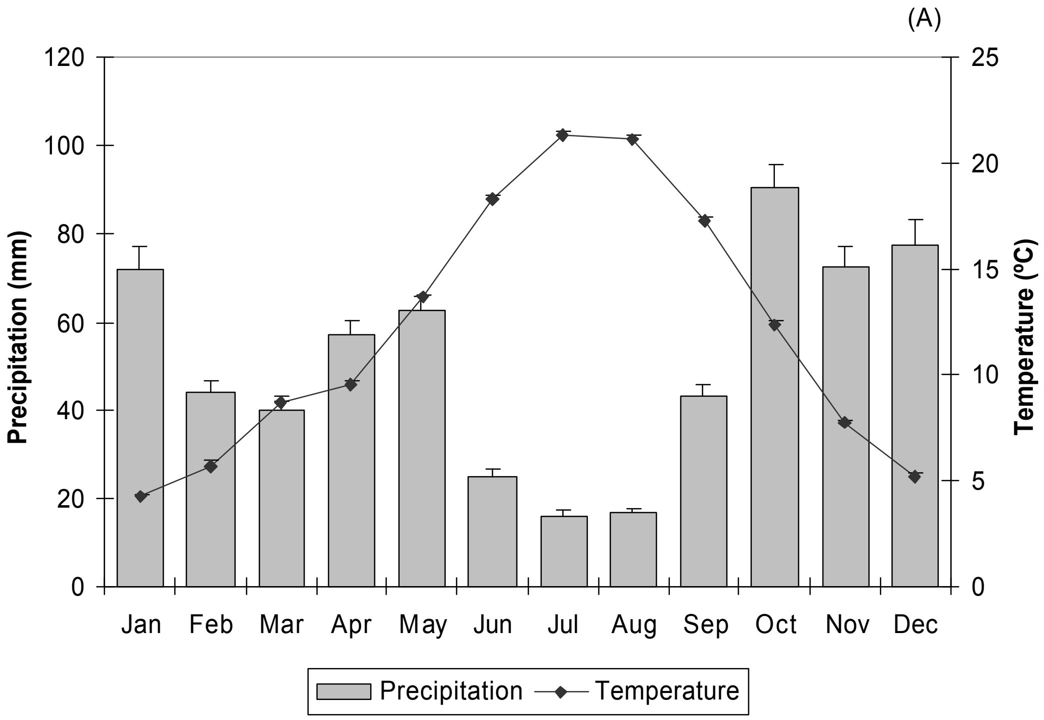
Figure captions

Fig. 1. Variation of precipitation and temperature over the 20-year period. (A) Monthly precipitation and mean monthly temperature (± SE). (B) Annual precipitation (± SE).

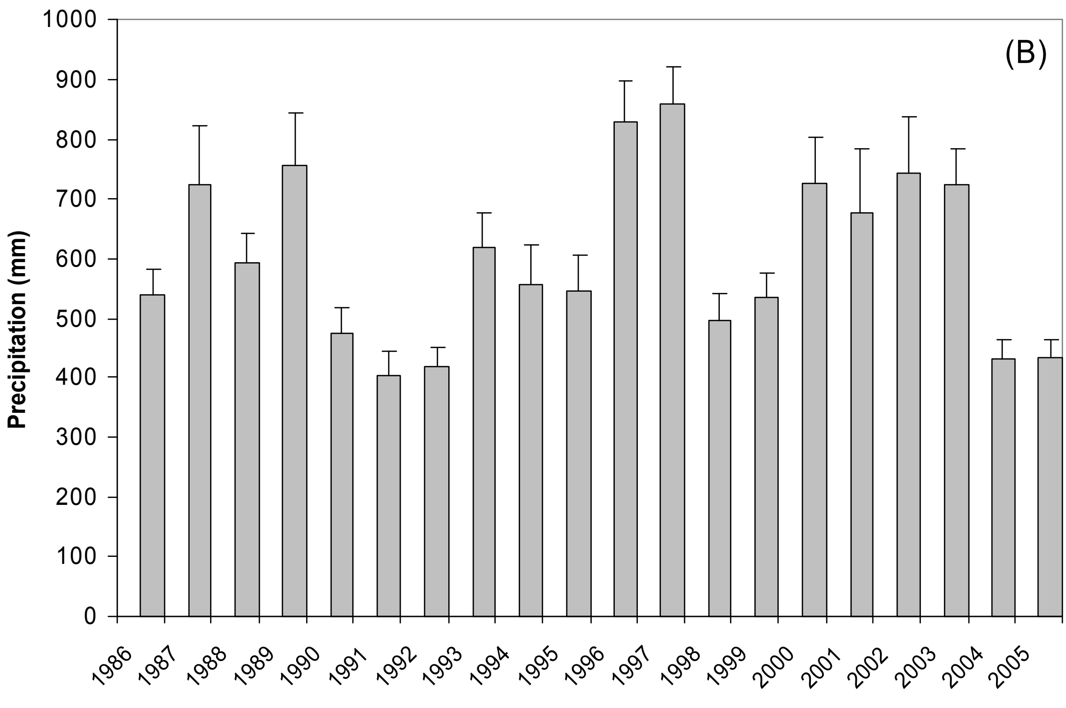
Fig. 2. Biomass (g/m^2) of total herbage, grasses, legumes and forbs in the upper and lower slope zones from 1986 to 2005. Values are means ± standard error of the mean.

Fig. 3. Concentration (g/kg) of protein, neutral detergent fibre (NDF), acid detergent fibre (ADF), lignin and digestibility (DMD) of semiarid grasslands in the upper and lower slope zones from 1986 to 2005. Values are means ± standard error of the mean.

Fig. 4. Relationships between total biomass on the upper (∆) and lower (■) zones and (*a*) precipitation from October to June, (*b*) Number of days with temperature below 0 ºC in November .


(A)
Precipitation (mm)
Temperature (ºC)
120
100
80
60
40
20
0
25
20
15
10
5
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Precipitation
Temperature

1


(B)
Precipitation (mm)
1000
900
800
700
600
500
400
300
200
100
0
1986
1987
1988
1989
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1991
1992
1993
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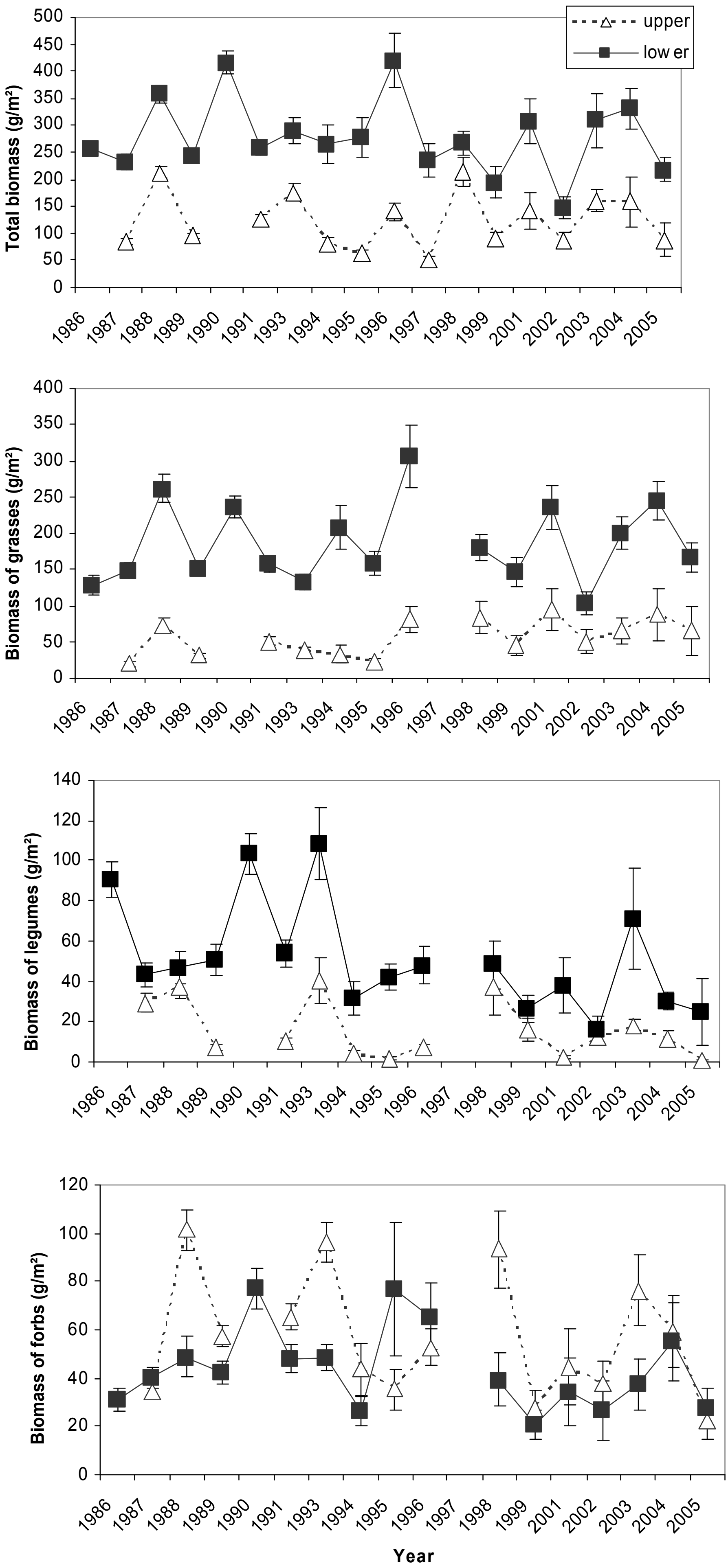
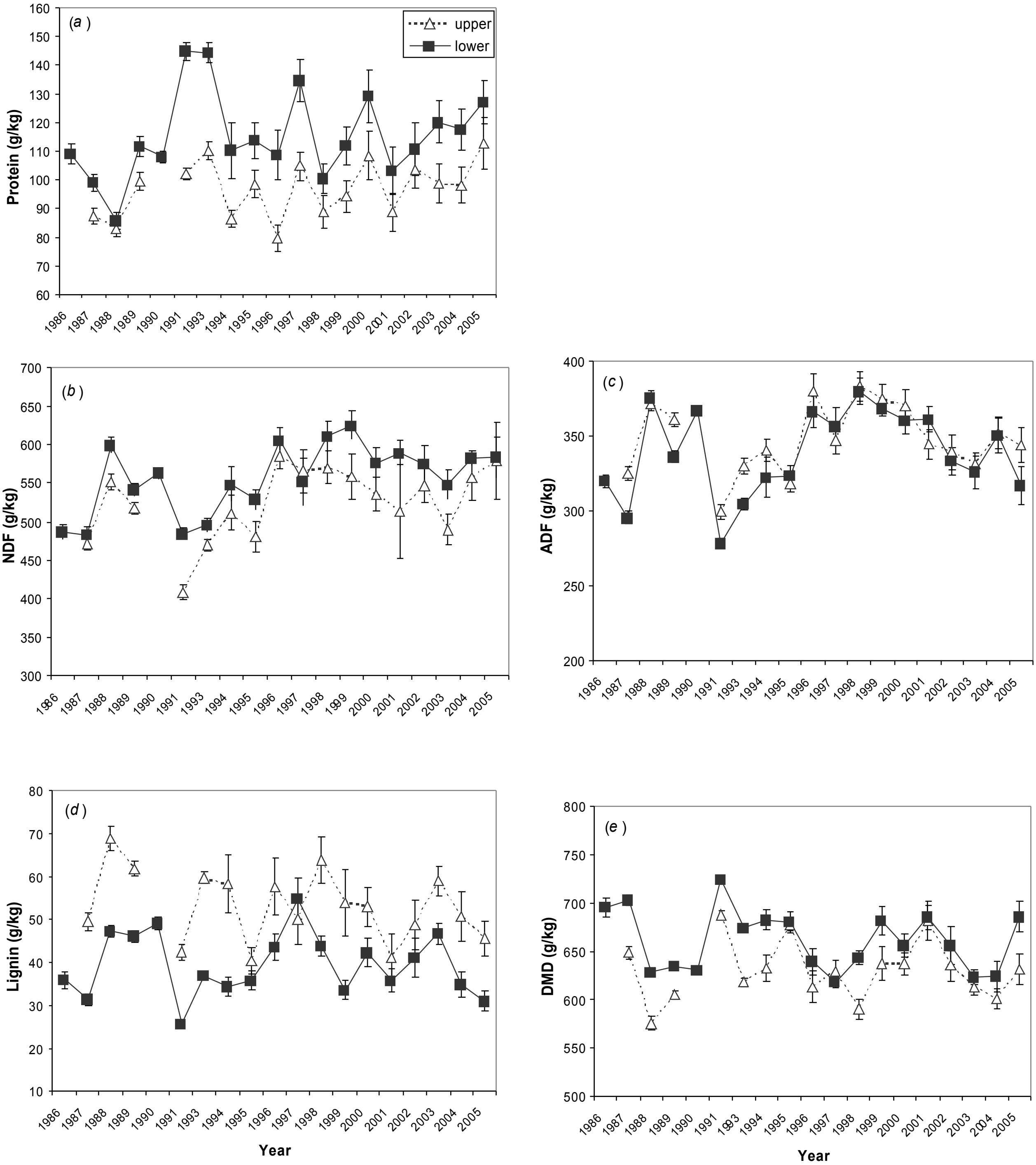
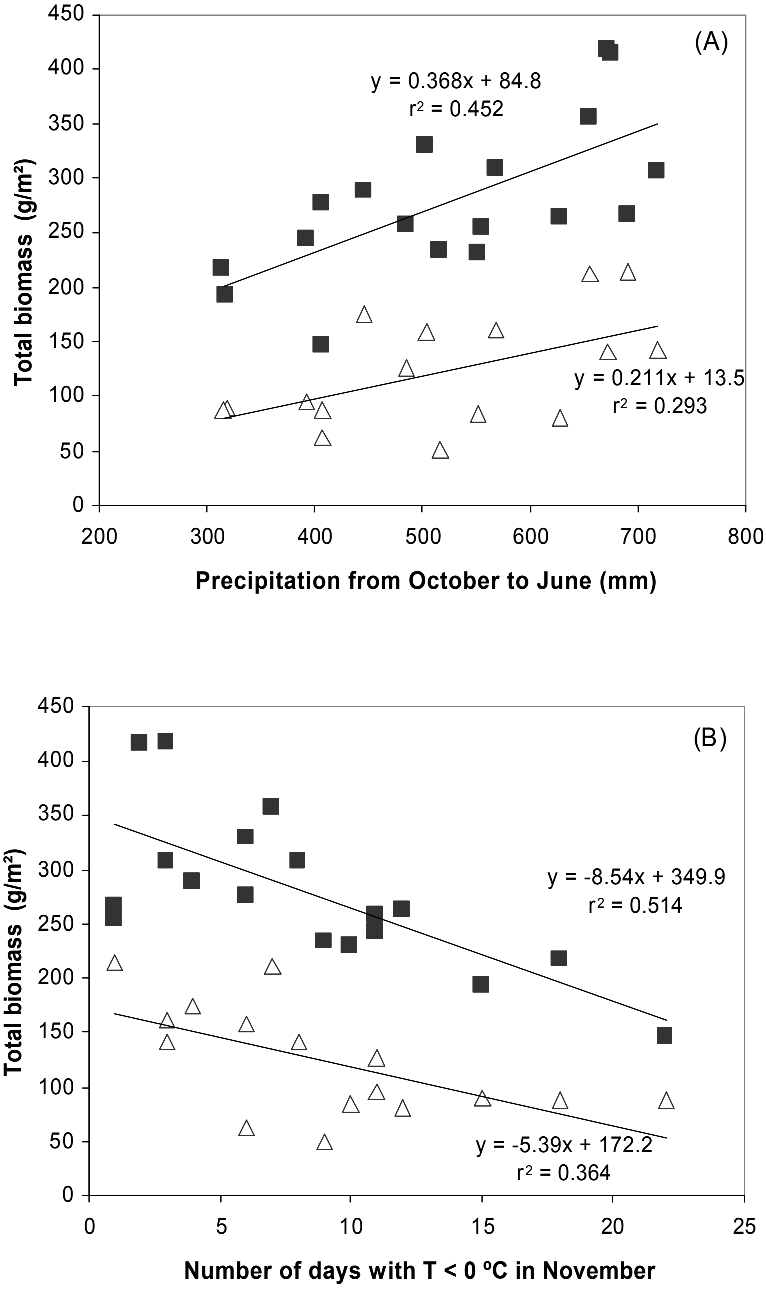
2002
2003
2004
2005

2


upper
lower
Total biomass (g/m²)
Biomass of grasses (g/m²)
Biomass of legumes (g/m²)
Biomass of forbs (g/m²)
Year

2


(a)
upper
lower
Protein (g/kg)
(b)
NDF (g/kg)
(c)
ADF (g/kg)
(d)
Lignin (g/kg)
Year
(e)
DMD (g/kg)
Year


(A)
y = 0.368x + 84.8
r² = 0.452
y = 0.211x + 13.5
r² = 0.293
Total biomass (g/m²)
Precipitation from October to June (mm)
(B)
y = -8.54x + 349.9
r² = 0.514
y = -5.39x + 172.2
r² = 0.364
Total biomass (g/m²)
Number of days with T < 0 ºC in November